# *Mysella gregaria* new species, a bivalve (Galeommatoidea: Montacutidae) commensal with an intertidal burrowing sea anemone from North Carolina, USA

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# ABSTRACT

*Mysella gregaria* new species (Bivalvia: Galeommatoidea: Montacutidae) is described from Wrightsville Beach, North Carolina. USA. Several individuals were collected from the body column of an intertidal burrowing unidentified actinian. The morphology of the shell and soft parts is described and compared with other species of the genus from the W. Atlantic Ocean and with other bivalves associated with solitary anthozoans. *Mysella gregaria* is a ctenidial brooder and specimens are either males or females; no true hermaphrodites were found. Contrary to many less social commensal bivalves, reproduction in *M. gregaria* does not involve sperm storage. We suggest that this may be correlated with the species' gregariousness.

*Additional Keywords:* Mollusca, reproduction, anatomy, sperm morphology, gregariousness.

## INTRODUCTION

During intertidal collecting on a muddy sand flat at Wrightsville Beach, North Carolina, USA, one of us (TF) collected a number of galeommatoidean bivalves from S-10 cm long specimens of an unidentified burrowing actinian. The host species was rare, as not more than an estimated 5–S specimens were found during occasional visits to the locality in the period from October 1970 through July 1975. Unfortunately, none of them were preserved for later identification. Only two of the collected actinians had commensal bivalves attached.

Many bivalves of the superfamily Galeonmatoidea have a commensal life style as they live together with species of bottom-dwelling marine invertebrate hosts such as other bivalves, polychaetes, sipunculans, echiurans, crustaceans, and echinoderms. Commensal associations between bivalves and solitary anthozoans are restricted to three known cases (Yamamoto and Habe, 1961; Ponder, 1971; Oliver, 1993) and it was therefore judged to be of interest to examine the present association more closely. The study has disclosed that the bivalves represent a new species of *Mysella* Angas, 1877, a genus that comprises both commensal and free-living bivalves and species that are commensal on certain conditions, free-living on other conditions (Ockelmann and Muus, 1978).

#### MATERIALS AND METHODS

Thirty-two bivalves were retrieved from the skin of a host specimen collected on 9 July 1975. The site of collection was a sandy mud tidal flat in Banks Channel, Wrightsville Beach, North Carolina, and the approximate coordinates are longitude 77.8° W and latitude 34.2° N. The anemones were dug from the lower intertidal zone during a spring low tide. The number associated with the second host and the date of collection was not noted. The behavior of the bivalves after removal from the host was not studied, but it was observed that they detached easily. Seventeen of the bivalves were preserved in Heidenhain's Susa for several hours. This procedure decalcifies the shells and the sizes given based on measurements of the mantle are therefore approximate. Three other bivalves were fixed in 70% ethanol and used for the description of the shell and for type material. Six specimens were embedded in Araldite and cut into 2-µm thick serial sections that were stained with toludine blue. Seven other specimens were embedded in Paraplast, sectioned. and the 8-µm thick serial sections stained with hematoxylin and eosin (H+E). Ultrathin sections were performed on the testis of one of the males. These sections

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were contrasted with uranyl acetate and lead citrate and examined in a JEOL 100SX electron microscope. Scanning electron micrographs were made using a JEOL JSM-6335F SEM. Photos of the type specimens of *Mysella casta* (Verrill and Bush, 1897) (USNM 77632) and *M. barbadensis* Dall, 1899 (USNM 95703) were used for comparison with *M. gregaria*. Shell length (SL) and height (SH) are given to the nearest 0.1 mm.

### SYSTEMATICS

Family Montacutidae Clark, 1855 Genus Mysella Angas, 1877

*Mysella* gregaria new species (Figures 1–20)

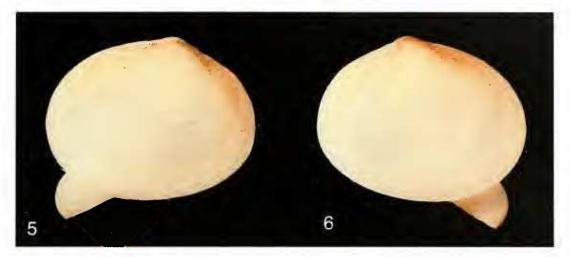
**Description:** SHELL (Figures 1–10): Observations were made on three shells. The SL of twenty measured specimens varied from 3.0 to 6.0 mm. The measurements SL×SH in the type material are  $4.5\times3.6$  mm,  $5.1\times3.8$  mm, and  $5.5\times4.3$  mm. The outline is almost perfectly oval, slightly higher in the anterior part, all margins being evenly rounded. The valves are relatively flattened, very thin, semitransparent, and with a light-brown to grey-brown periostracum, which is darkest in the dorsal

part. There are no coatings of ferruginous deposits. The surface is smooth, with very fine commarginal lines and even finer radial striae. No growth checks were ever visible. The interior surfaces of the valves are polished. The umbos are not very prominent and placed slightly toward the posterior region. In the right valve there are two diverging teeth; the anterior tooth is elongatesubtriangular and more prominent than the narrower, posterior one. They are separated by a stout ligament placed immediately below umbo in a triangular resilifer. The left valve is edentulous but has a produced dorsal margin that fits into the teeth of the right valve. The anterior adductor scar is subtriangular, the posterior more oval, both fused with the respective foot retractor scars. The pallial line is relatively broad and lacks a pallial sinus.

MANTLE (Figure 11): The mantle folds are fused far behind and for a short distance to separate the mantle opening into an inhalant-pedal aperture and an exhalant aperture. While the first forms a long slit along the fourfifths of the length of the ventral side, the exhalant aperture is very small and located far posteriorly. Since live animals were not observed, we do not know whether, or to which extent, the mid mantle fold may cover the outside of the shell or whether there are any siphons. The mantle edges bear minute papillae that are most distinct



Figures 1–4. Mysella gregaria. Cleaned shell of holotype. 1. Right shell seen from inside. 2. Right shell seen from outside. 3. Left valve seen from inside. 4. Left shell seen from outside. Shell length 5.1 mm.

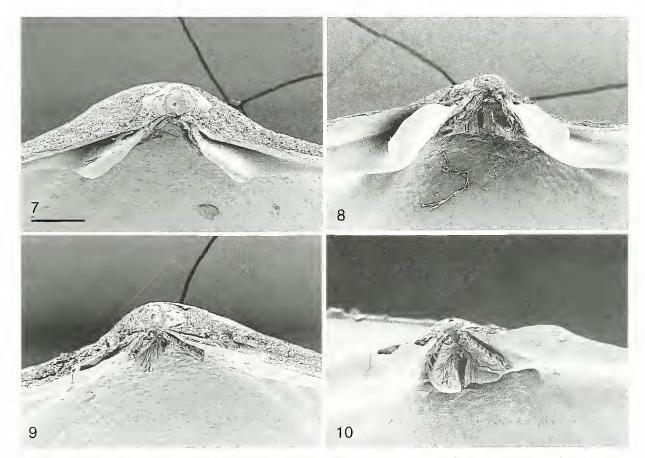


Figures 5, 6. Mysella gregaria. Paratype, outside view of left (5) and right sides (6). Shell length 4.5 mm.

in the dorso-anterior sector. A typical, ciliated rejection fold is located just anterior to the end of the inhalantpedal opening.

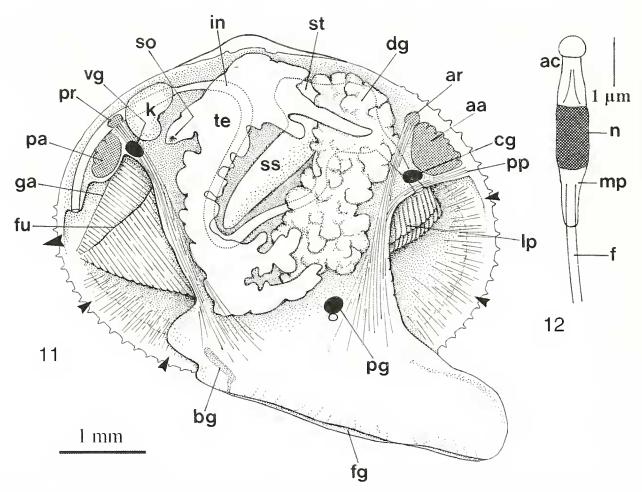
MUSCULATURE (Figures 11, 13): The anterior adductor muscle is the larger of the two and is subtriangular in

outline, whereas the smaller posterior adductor is more oval. A small pedal protractor muscle is located ventrally and clearly outside the anterior adductor muscle. The two pedal retractor muscles are equally large and of moderate size. They terminate in the base of the foot,



Figures 7–10. *Mysella gregaria*. Holotype, SL 5.1 mm. Scanning electron micrographs of right hinge seen in direct view (7) and slightly tilted from below (8) and of left hinge seen in direct view (9) and slightly tilted from below (10). Scale bar represents  $200 \ \mu m$ .

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Figures 11, 12. *Mysclla gregaria*. 11. Anatomy of male, right valve, mantle and gill removed, heart and pericardium omitted. 12. Light microscopic representation of sperm cell. Abbreviations: **aa**, anterior adductor muscle; **ac**, acrosome; **ar**, anterior pedal retractor muscle; **bg**, byssus gland: **cg**, cerebral ganglion; **dg**, digestive gland: **f**, flagellum; **fg**, foot groove; **fu**, fusion of left and right demibranch behind visceral mass; **ga**, gill axis; **in**, intestine; **k**, kidney; **lp**, labial palps; **mp**, middlepicce; **n**, nucleus; **pa**, posterior adductor muscle; **pg**, pedal ganglion and statocysts: **pp**, protractor pedis muscle: **pr**, posterior pedal retractor muscle; **so**, sexual opening: **ss**, style sae; **st**, stomach; **te**, testis; **vg**, visceral ganglion. Arrowheads indicate water entering along the inhalant-pedal opening and exiting through the exhalant opening.

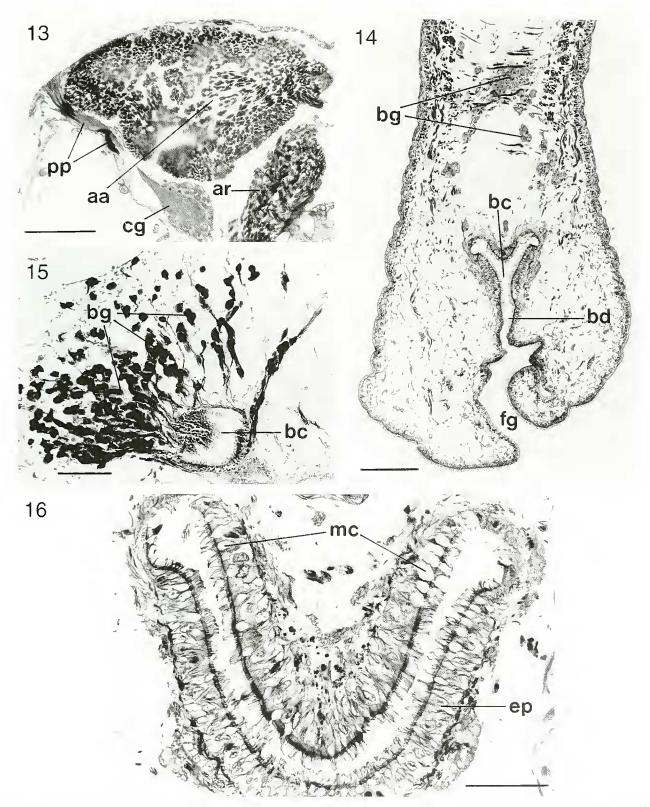
while only a few fibers spread further into the foot. There are almost no muscle fibers serving the byssus gland.

FOOT AND BYSSUS GLAND (Figures 11, 14-16): In preserved specimens, the foot extends forward and a little beyond the shell margin. It is bluntly rounded in front. The ventral side is distinctly ciliated and has a furrow that extends from in front of the heel to tip of the foot. In some specimens a blackish pigment spot can be seen at the very tip of the foot. The very small byssus cavity appears Y-shaped in transversal sections as it consist of a right and left slit which both discharge into the median furrow by way of a single duct. The lining epithelium is composed of a mixture of ciliated and of mucous-producing goblet cells. A group of more distant glandular cells terminate between the cells of the byssus cavity cpithelium through long, slender ducts. Although such cells are normally involved in the formation of byssal threads, none were ever seen either in sections or on whole animals. The nature of the glandular epithelium indicates that slime threads, rather than normal byssal threads are produced by the byssus gland.

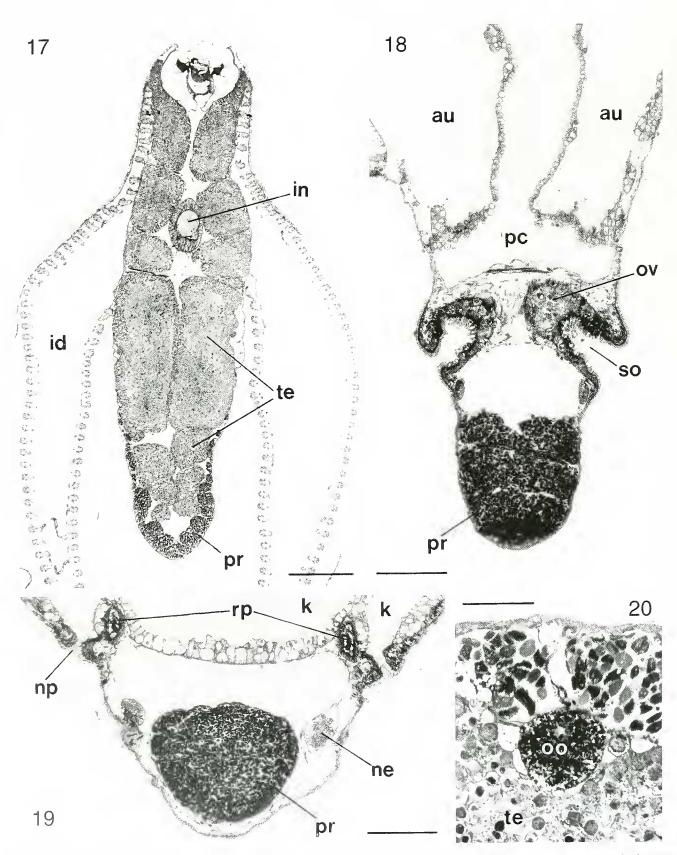
GILLS (Figures 11, 17): The gill axis, which runs from near the umbo, has an oblique course backward. Each gill is triangular. An outer demibranch is entirely absent and only the inner one is present. The ascending lamellae of the left and right demibranch are fused behind the foot, more anteriorly to the lateral sides of the visceral mass. Both gills are fused to the mantle edges immediately in front of the exhakint opening. A food groove is only present along the ventral edges of each gill. Interlamellar junctions are present, but they are very few, whereas interfilamentary bridges are numerous and occur regularly. Right and left hypobranchial glands of normal size occur well inside the exhalant aperture. A pair of relatively large labial palps lies on either side of the month. Their opposing surfaces are provided with 9–10 ciliated ridges.

ALIMENTARY CANAL (Figure 11): The esophagus is a

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**Figures 13–16.** *Mysella gregaria.* **13.** Sagittal section of a male (SL 3.0 mm) showing the course of the protractor pedia muscle (**pp**). **14.** Transverse section of a male (SL 4.3 mm) through the foot and the opening of the byssus cavity (bc). **15.** Byssus gland cells (**bg**) opening into byssus cavity **16.** Transverse section through byssus cavity of the male shown in **Fig. 14.** Abbreviations: **aa**, anterior adductor muscle; **ar**, anterior pedal retractor muscle; **bc**, byssus cavity; **bd**, byssus duct; **bg**, byssus glandular cells; **cg**, cerebral ganglion: **ep**, epithelium of byssus cavity; **fg**, foot groove; **mc**, mucous cells. **2**-μm thick Araldite sections stained with toluidine blue (**13. 14** and **16**) and S-μm thick paraplast sections stained with H+E (**15**). Scale bars represent 100 μm (**13–15**) and 30 μm (**16**).



**Figures 17–20.** *Mysella gregaria.* Transversal section of male (SL 4.3 mm) (17) and of female (18, 19). 20. Testis with abortive occyte (oo). Abbreviations: **au**, auricles; **id**, inner demibranch: **in**, intestine; **k**, kidney; **ne**, nerve; **np**, nephridiopore; **ov**, posterior wall of ovary; **pe**, pericardial cavity; **pr**, posterior pedal retractor muscle; **rp**, renopericardial canal; **so**, sexual opening; **te**, testis. 2-μm thick Araddite sections stained with toluidine blue. Scale bars represent 200 μm (17), 100μm (18, 19) and 50 μm (20).

short eurved tube. The stomach is relatively capacions and heavily cuticularized. The style sac forms a wide posterior continuation from the stomach, is elongated conical, nearly as long as the stomach, and directed postero-ventrally. It is placed within the right side of the visceral mass. The intestine leaves from the underside of the stomach near its connection to the style sac, runs alongside the style sac and forms a loop around its tip, then turns dorsally between left and right parts of the gonad to loop backwards to the rectum The boundary between the ciliated intestine and the unciliated rectum is marked by a sharp transition zone dorsal to the posterior adductor.

The digestive gland is mainly located ventral to the stomach and around the posterior part of the esophagus. In addition to a large ventral communication with the stomach, there are also smaller openings into it.

REPRODUCTIVE SYSTEM (Figures 11, 17, 18, 20): Eight sectioned hivalves (SL = 3.0-5.6 mm) were males, while three other sectioned bivalves (SL = 4.1-6.0 mm) were females. No truly hermaphroditic specimens were found, but a few mature oocytes were present in the testis of one of the males (Figure 20).

All males were sexually mature. The very large testis occupies the posterior half of the visceral mass being replaced more anteriorly by the style sac, stomach, and digestive gland. The general shape as seen in decalcified specimens is relatively constant. A large undivided posterior portion gives rise to right and left halves that surround the intestine and extend ventrally to send a few short branches forward. Two other forwardly directed finger-shaped branches embrace the stomach. The paired spermiducts issue from the most posterior, undivided part of the testis. They are short but have prominent funnel-shaped and heavily ciliated openings into the suprabranchial chamber. Spermatogenesis proceeds everywhere along the walls of the different portions of the testis. There is no special chamber for storing the mature sperm which, in a non-orientated manner accumulate in huge numbers in the central parts of the different portions of the testis. Many spherical to ovoid cells,  $5-7 \ \mu m$ in diameter, lie scattered among the mature sperm. These cells have a centrally placed nucleus plus one or two inclusions. We were unable to discover how these cells arise and if they are in the any way associated with the spermatogenesis.

Because of the insufficient fixation the TEM micrographs were of low quality. They nevertheless show enough details to illustrate the general ultrastructure of the flagellate sperm cells (Figure 11, B). The acrosome is 1.4–1.5  $\mu$ m long and basally (near the nucleus) 0.6  $\mu$ m broad. It is divided into a terminal subspherical body (0.4×0.6  $\mu$ m) and a slightly tapering acrosomal vesicle, which is basally deeply invaginated to accommodate a filamentous subacrosomal material. The nucleus is 0.7– 0.5  $\mu$ m across and 1.2–1.3  $\mu$ m in length. The 1.4–1.5  $\mu$ m long middle piece was extremely ill-preserved without any identifiable mitochondria but seems from a broad base near the nucleus to taper backwards. The female sexual openings (Figure 18) are identical in size and structure to those of the male. Two females were obviously spent, but one of them had retained a few abortive occytes (diameter ca. 60  $\mu$ m) within the ovary and a few embryos in the suprabranchial chamber. Except for this, none of six decalcified but unsexed specimens examined in transparent light (SL = 4.0–5.6 mm) were brooding ova or larvae. No structures for storing foreign sperm were found in any of the sectioned bivalves.

EXCRETORY SYSTEM (Figures 11, 18, 19): Left and right halves of the kidney communicate in the median plane for a short distance. Each one is composed of several smaller and larger sacs with glandular walls. Anterolaterally the kidney opens directly to the suprabrancial chamber through two ciliated nephroducts, which are uncharacteristically short and have porous nephridiopores placed not far from the genital opening. Rather far behind within the kidney, two long straight and heavily ciliated renopericardial canals run forward to open into the forward and ventral part of the pericardium.

HOST RELATIONS: All 32 individuals were attached onto the body column of a single sea anemone, whereas the number attached to a second host was not noted. None were found on any of the other host specimens from the same site, which suggests that the species is gregarious. It was observed that the attachment to the host was very loose as several of the bivalves had fallen off during the collection. This corresponds with the conclusion that no true byssus threads are produced and that attachment rather takes place by means of shime threads.

**Holotype:** BIV-445 (Zoological Museum, University of Copenhagen), a cleaned shell, SL = 5.1 mm.

**Paratypes:** BIV-446, a shelled animal, SL = 4.5 mm; USNM 1107828 (National Museum of Natural History, Washington, DC), a shelled animal, SL = 5.5 mm; all from type locality, 9 July 1975.

**Type Locality:** Banks Channel, Wrightsville Beach, North Carolina, USA. (ca. 77.8° W, 34.2° N), lower intertidal zone during spring low tide, sandy mud substratum. 9 July 1975. Thirty-two specimens were attached to a single host.

**Etymology:** the species name is derived from the Latin *grex*, flock, and refers to the gregarious life style of the new species.

#### DISCUSSION

**Identification:** The details of the shell and hinge allocate the species into the genus *Mysella* (family Montacutidae) and indicate that it is close to the North Atlantic *M bidentata* (Montagu, 1803). In *M. gregaria* the protractor pedis muscle is inserted immediately ventral to the anterior adductor as in *M. bidentata* (Montagu, 1803) and in *Montacutona compacta* (Gould, 1861), in contrast to the condition in another group of mon-

tacutids, in which it splits the adductor in dorsal and ventral portions (Jespersen et al., in press). Mysella has often been combined with Rochefortia Velain, 1877, but the two differ with respect to the dimensions of the teeth of the right valve (Coan et al., 2000; Holmes et al., 2006). In species of Mysella the right valve has a stout transverse tooth anterior to the resilifer and a posterior tooth is either small or absent. In *Rochefortia* the right valve has two subequal diverging teeth, which would place *M. gregaria* in *Rochefortia*. The distinction ignores the available soft anatomical characters which, especially in species with a *Rochefortia* type of hinge, vary considerably: A small outer demibranch is present in some (M,tumida (Carpenter, 1864), M. verrilli (Dall, 1899), and M. sovaliki McGinitie 1959), absent in other (M. bidentata and M. gregaria). The esophagus is a simple tube in all the species except for *M. verrilli*, in which it forms a suctorial proboscis. Foreign sperm are either not stored (*M. gregaria* and *M. verrilli*), attached directly to the gill surface (M. tumida), or stored in an unpaired pouchshaped seminal receptacle within the visceral mass (M. bidentata) or in paired receptacles in the outer demibranch (M. sovaliki). A new definition of the genus Mysella will probably be called for as additional data on the anatomy of a wider range of species will bring about a complete rearrangement of the genus and its included species.

From the described species of *Mysella* from the East American waters, M. gregaria may be distinguished by the following characters: M. planulata (Stimpson, 1857) has a very prominent hinge and the umbo is placed more posteriorly. It attaches to buoys and wharf pilings or occurs in muddy sand of the Zostera community (Abbott, 1974; Franz, 1973). In Mysella ovata (Jeffreys, 1881) the umbo is extremely protruding and placed far posteriorly. It occurs in depths of 183 to 287 m. The shell of M. triquetra (Verrill and Bush, 1898) is equilateral and the posterior part of the shell is distinctly rostrate, not evenly rounded. Mysella verrilli, a deep water species, has the umbo placed far posteriorly and the esophagus is developed as a suctorial proboseis (Allen, 2000). In M. striatula (Verrill and Bush, 1898), both teeth are delicate and very narrow, the anterior tooth is shorter, and the very small numbo is located more posteriorly than in M. gregaria. The shell of the following two species were studied from photos provided by the National Museum of Natural History, Smithsonian Institution (USNM): The anterior part of a left valve of M. barbadensis Dall, 1899 (USNM 95703) is almost three times as long as the posterior part (in contrast to the claim that it is shorter as described by Dall, who obviously mistook a left valve for a right one). The left valve of the type of M. casta Verrill and Bush. 1898 from North Carolina (USNM 77632) is more elongate (SII:SL = 7:10) than the values of M. gregaria (SH:SL = 7.8:10) and the anterior end relatively longer. Nevertheless, among the East American species, the shell of M casta is the one most similar to M. gregaria.

Comparison with North Atlantic/Arctic species of Mysella: Conchologically M. gregaria resembles M. bidentata (Montagu, 1803) but differs anatomically in that the latter has an unpaired seminal receptacle and dimorphic sperm (Jespersen and Lützen, 2001). The shell of *M. cuneata* (Verrill and Bush, 1898) is distinctly asymmetrical, as the right valve shows a slight concavity with a consequent skewness along the ventral margin (Gage, 1968). In M. tumidula (Jeffreys, 1866), the posterior shell margin is distinctly angular, not evenly rounded. Mysella moelleri (Mörch, 1877) and M. sovaliki both differ from *M. gregaria* in the hinge structure and, more significantly, in having preserved a small outer demibranch (Petersen and Liitzen, in press). Mysella planata (Dall in Krause, 1885) has a thick shell, in which the left valve has the dorsal line modified into two teeth, and the right valve shows only one, anterior tooth (van Aartsen, 1996).

Comparison with Other Bivalves Associated with Anthozoans: Commensalism between bivalves and anthozoans is rare. Nipponomontacuta actinariophila Yamamoto and Habe, 1961, is small Japanese bivalve that has been found attached immediately outside the ring of tentacles of *Halcampella maxima* Hertwig (Actiniaria: Halcampoididae). Details of the relationship are not known, except that three specimens sitting close together outside the ring of tentacles were illustrated by Habe (1973). Although the outline of the shell and the position of the umbo in *N. actinariophila* are somewhat similar to the studied species, the hinges are clearly different, as teeth are only present in the left valve in N. actiniariophila, not, as in M. gregaria, on the right valve. Montacutona ceriantha Ponder, 1971, from Cerianthus sp. (Ceriantharia) in Moreton Bay, E Australia, is easily separated from M. gregaria in that each valve has four cardinal teeth and a small outer demibranch is present. Furthermore, M. ceriantha is attached to the interior of the tube of the host, not to the body, and in a small numbers (Table 1) (Ponder, 1971). A third bivalve, Halcampicola tenacis Oliver, 1993, from Rottnest Island off Perth, SW Australia has a hinge similar to *Montacuta*, the right valve with a strong anterior cardinal merging with a submarginal lateral ridge and an obsolete posterior cardinal. The left valve has anterior and posterior strongly projecting marginal extensions which fit into the right valve (Oliver, 1993). Besides, the ligament has a lithodesma and there is a small outer demibranch. A single bivalve was found on each of six hosts (*Halcampoides* sp., Actiniaria: Halcampoididae) among 20 collected. It seems fairly obvious that all four anthozoan-associated bivalve species are not specifically interrelated.

**Reproduction:** Eight of the sectioned bivalves (SL = 3.0-5.6 mm) were sexually mature males and three other (SL = 4.1-6.0) were females. The females were spent but one had retained a few embryos in the suprabranchial chamber which shows that this species, like other gale-ommatoideans, is a ctenidial brooder. A few mature oocytes, left over from a previous ovulation, were present in

Bivalve species	Mean no. per host specimen	Host species	Reproductive specializations	References
Montacuta percompressa	1	tIolothurioidea	tt	Fox et al., 2007
Peregrinamor ohshimai	1	Crustacea	sr, dw	Lützen et al., 2001a
Salpocola philippinensis	1	Sipuncula	tt?	Lützen et al., in press
Halcampicola tenacis	1	Anthozoa	?	pers. comm. (Graham Oliver)
Litigiella pacifica	1-3	Sipuncula	sr	Lützen and Kosuge, 2006
Montacutona ceriantha	1.8	Anthozoa	sr	Ponder, 1971
Entovalva lessonothuriae	< 2	Holothurioidea	sp	Kato, 1998; Lützen et al., 2005
Pythina arcuata	ca. 2	Brachiopoda	sť	pers. comm. (IL)
Anisodevonia ohshimai	1.8-2.7	11olotur <sup>i</sup> oidea	sp	Kosnge, 2001; Lützen et al., 2003
Nipponomysella subtruncata	2.5	Sipuncula	sr, ss	Lützen et al., 2001b
Tellimya ferruginosa	< 3	Echinoidea	tt	Fox et al., 2007
Mioerycina coarctata	3.8	Sipuncula	sr	Gage, 1979
Mysella cuneata	5	Sipuncula	sr	Gage, 1968

**Table 1.** Mean number of commensal bivalves per host specimen and reproductive specializations in montacutid bivalves. Abbreviations: **dw**, dwarf males; **sp**, spermatophores; **sr**, seminal receptables; **ss**, sperm sacs; **tt**, testis transplantation.

one of the males, which could indicate that females may change sex and that the species shows hermaphroditic tendencies. The species in all probability reproduces by outcrossing, since none of the sectioned bivalves showed truly simultaneous hermaphroditic characteristics.

All galeommatoideans brood the ova in a ctenidial brooding chamber consisting of the inner and, if present, the outer demibranch. This is also where fertilization takes place. In a normally-filtering bivalve the gills and the currents they generate do not favor a casual intake of sperm suspended in the water. The ciliary activity of the gills probably functions as a barrier for penetration of most sperm cells and the only other access to the brooding chamber is against the flow of filtered water expelled through the exhalant aperture. Many species have overcome these difficulties by bulk transfer of sperm in containers of different nature to the female's suprabranchial chamber (see O Foighil, 1985a, for a review). Exactly how they do this is not understood except in a single case. (O Foighil, 1985b). Some species have minute dwarf males that are permanently and intimately associated with the much larger female and still other produce sperm of two types that form spermatozeugmata. Some of that spermatozeugmata is probably capable of independent mobility. None of these methods of a precise transfer of sperm occur in M. gregaria. The testis is exceptionally large in the species, and we speculate that the resulting high production of sperm cells may compensate for the inevitable loss suffered during the transfer between the opposite sexes of sperm cells that are simply broadcast into the water.

Sperm transferred to a female (or hermaphrodite) are often stored for a considerable period either on the gills or in seminal receptacles of various types and location. We think it is likely that there may be some correlation between the presence or absence of storing devices and the chance of encountering bivalves of the opposite sex. The commensal galeonmatoid bivalves are sequestered along with their host into a microhabitat that they probably never leave. A few examples show that the number of montacutid bivalves present per host (or host burrow) is usually small (Table 1). Except for *H. tenacis*, which has not been anatomically studied, all these species have evolved various measures that allow long-time storage of sperm in the female (or hermaphrodite), which effectively enhance the chances that spawned ova can be fertilized even if no sexual partners are around. Conversely, in a highly social species, like M. gregaria, such mechanisms are evidently much less needed. It would be interesting to study the relation between the sizes of the micro-populations in other Montacutidae that neither exhibit sperm transfer nor sperm storage. Unfortunately, besides the present species, the known cases are limited to two species with unknown spatial distribution, Tellimya tenella (Lovén, 1846) and Mysella moelleri (Fox et al. 2007; Petersen and Lützen, in press).

The present study has shown the need for further information on the anatomy as a tool of a better understanding of the taxonomy, which, to a much too large extent, has been based only on shell characters. More data are also wanted on the numerical relations between hosts and commensals and, above all, analyses on the sexual behavior of commensal bivalves are in very high demand.

## ACKNOWLEDGMENTS

The study was supported by a grant to JL and ÅJ from the Danish National Science Foundation (no. 51-00-0278). We are grateful to Mr. Bjarne Bisballe, Zoological Museum, Copenhagen, for operating the Scanning electron microscope and to Mr. Gert Brovad, same institution, for photographic assistance. We further thank Dr. Graham Oliver, National Museum of Wales, Cardiff, UK, for providing information about the occurrence of *Halcampicola tenacis* on its host.

#### LITERATURE CITED

Abbott, R. T. American Seashells. 1974. 2nd edition. Van Nostrand-Reinhold Co., New York, pp. 663

- Allen, J. A. 2000. An unusual suctorial montacutid bivalve from the deep Atlantic. Journal of the Marine Biological Association of the United Kingdom 80: 827–834
- Coan, E. V., P. V. Scott and F. R. Bernard. 2000. Bivalve Sea Shells of Western North America. 764 pp. Santa Barbara Museum of Natural History, Santa Barbara.
- Fox T. H., Å. Jespersen and J. Lützen. 2007. Sperm transfer and reproductive biology in species of hermaphroditic bivalves (Galeonmatoidea: Montacutidae). Journal of Morphology 268: 936–952.
- Franz, D.R. 1973. The ecology and reproduction of a marine bivalve, *Mysella planulata* (Erycinacea). Biological Bulletin Woods Hole 144: 93–106.
- Gage, J. D. 1968. The mode of *Mysella cuncata*, a bivalve commensal with *Phascolion strombi* (Sipuncuidea). Canadian Journal of Zoology 46: 919–934.
- Gage, J. D. 1979. Mode of life and behaviour of *Montecuta pluascolionis*, a bivalve commensal with the sipunculoidea *Pluascolion strombi*. Journal of the Marine Biological Association of the United Kingdom 59: 635–657.
- Habe, T. 1973. Halcampella maxima Hertwig, host of Nipponomontecuta actinariophila Yamamoto & Habe. Venus 31: 157.
- Holmes, A. M, J. Gallichan, and H. Wood. 2006. Coracuta obliquata n. gen. (Chaster, 1897) (Bivalvia: Montacutidae) —first British record for 100 years. Journal of Conchology 39 (2): 151–158.
- Jespersen, Å and J. Lützen. 2001. Ultrastructure of the seminal receptacle and the dimorphic sperm in the commensal bivalve *Mysella bidentata* (Veneroida; Galeonmatoidea; Montacutidae). Acta Zoologica 82: 107–115.
- Jespersen, Å, J. Lützen, and P. G. Oliver. In press. Morphology, biology and systematic position of *Epilepton clarkiae* (Clark, 1852) (Galeommatoidea: Montacntidae), a bivalve commensal with sipunculans. Journal of Conchology.
- Kato, M. 1998. Morphological and ecological adaptations in Montacutid bivalves endo- ectosymbiotic with holothurians. Canadian Journal of Zoology 76: 1403–1410.
- Kosnge, T. 2001. Écological notes on the populations of the galeommatid bivalve Anisodevonia olushimai in Ishigaki Island, Southern Japan. Biological Magazine, Okinawa 39: 5–10.
- Lützen, J., H. Sakamoto, A. Taguchi, and T. Takahashi. 2001a. Reproduction, dwarf males, sperm dimorphism, and life cycle in the commensal bivalve *Peregrinamor olushimai* Shoji. Malacologia 43: 313–325.

- Lützen, J., T. Takahashi, and T.Yamaguchi. 2001b. Morphology and reproduction of *Nipponomysella subtruncata* (Yokoyama), a galeommatoidean bivalve commensal with the sipunculan *Sipluonosoma cumanense* (Keferstein) in Japan. Journal of Zoology 245: 429–440.
- Lützen, J., M. Kato, T. Kosuge, and D. Ó Foighil. 2005. Reproduction involving spermatophores in four bivalve genera of the superfamily Galeonmatoidea commensal with holothurians. Molluscan Research 25: 99–112.
- Liitzen, J. and T. Kosuge. 2006. Description of the bivalve LittigicIla pacifica n. sp. (Heterodonta: Galeonmatoidea: Lasaeidae), commensal with the Sipunculan Sipunculus nudus from the Ryukyu Islands, Japan. Venus 65: 193– 203.
- Lützen, J., T. Kosuge, and Å. Jespersen. In press. Morphology of the bivalve Salpocola philippinensis (Habe and Kanazawa, 1981), new genus (Galeonmatoidea: Lasaeidae), a commensal with the sipunculan Sipunculus nudus from Cebu Island, the Philippines. Venus.
- Ockelmann, K. and K. Muns. 1978. The biology, ecology and behaviour of the bivalve *Mysella bidentata* (Montagn). Ophelia 17: 1–98.
- Ó Foighil, D. 1985a. Form function, and origin of temporary dwarf males in *Pseudopythina rugifera* (Carpenter, 1864) (Bivalvia: Galeonmatacea). The Veliger 27: 245–252.
- Ó Foighil, D. 1985b. Sperm transfer and storage in the brooding bivalve *Mysella tumida*. Biological Bulletin Woods Hole 169: 602–614.
- Oliver, P. G. 1993. A new bivalve associated with a burrowing sea anemone. *Halcampicola tenacis* gen. sp. nov (Galeommatoidea: Montacutidae) on *Halcampoides* sp. (Anthozoa: Antipatharia: Halcampoididae). West Australian Museum, Perth, 1993: 255–265.
- Petersen, G. H. and J. Lützen. In press. Morphology of Mysella moclleri (Mörch. 1877) and Mysella sovaliki MacGinitie, 1959 (Bivalvia: Galeommatoidea: Montacutidae), with notes on their biology. Steenstrupia, Copenhagen.
- Ponder, W. F. 1971. Montacutona ceriantha n.sp., a commensal leptonid bivalve living with *Cerianthus*. Journal de Conchyliologie, Paris 109: 15–25.
- Van Aartsen, J. J. 1996. Galeommatacea and Cymiacea. Part 2. Conchiglia 28: 27–53
- Yamamoto T. and T. Habe. 1961. Nipponomontacuta actinariopluila gen. et sp. nov., a new commensal bivalve of the sea anemone. Seto Marine Biological Laboratory 9: 265–266.